Defining geo-habitats for groundwater ecosystem assessments: An example from England and Wales

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Abstract

Groundwater ecosystems comprising micro-organisms and metazoans provide an important contribution to global biodiversity. Their complexity depends on geology, which determines the physical habitat available, and the chemical conditions within it. Despite this, methods of classifying groundwater habitats using geological data are not well established and researchers have called for higher resolution habitat frameworks.

In this paper a novel habitat typology for England and Wales is proposed, which distinguishes 11 geological habitats (geo-habitats) on hydrogeological principles and maps their distribution. Hydrogeological and hydrochemical data are used to determine the characteristics of each geo-habitat, and demonstrate their differences. Using these abiotic parameters, a new method to determine abiotic habitat quality is then developed.

The geo-habitats had significantly different characteristics validating the classification system. Karstic and porous habitats generally had higher quality than fractured habitats. All geo-habitats were highly heterogeneous, containing both high quality habitat patches that are likely to be suitable for fauna, and areas of low quality that may limit faunal distributions. Overall, 70 % of England and Wales are covered by lower quality fractured habitats, with only 13 % covered by higher quality habitats. The main areas of high quality habitats occur in central England as north-south trending belts, possibly facilitating dispersal along this axis. They are separated by low quality geo-habitats that may prevent east-west dispersal of fauna. In south-west England and Wales suitable geo-habitats occur as small isolated patches. Overall, this paper provides a new national-scale typology that is adaptable for studies in other geographic areas.

1. Introduction

The earth's rocks and groundwater form unique, important habitats. Obligate groundwater invertebrates (called stygobites), and sometimes vertebrates, are the top-level consumers in these truncated communities. They feed on a variety of organisms, including protozoans, microbes and fungi (Gibert et al., 1994; Boulton et al., 2008; Weitowitz, 2017). These groundwater communities are likely to be important for their role in biogeochemical cycling and pollutant attenuation (Mattison et al., 2002, 2005). Stygobites also make a unique contribution to biodiversity because they are not found in other habitats, and have high rates of endemism and ancient ancestral lineages (Finston & Johnson, 2004; Lefebure et al., 2007; McInerney et al., 2014). Understanding the processes shaping groundwater ecosystems is important because they may be impacted by anthropogenic stressors, such as water abstraction, changes in water flow patterns, and the leaching of agrochemicals (Klove et al., 2011; Foster et al., 2016).

Groundwater ecosystems primarily depend on geology, which provides the physical habitat and determines hydrochemistry (Datry et al., 2005; Hahn, 2006; Maurice & Bloomfield, 2012). Three types of physical structures are available as groundwater habitats: Pore spaces, fractures, and karstic voids / caves. The habitat quality (i.e. their ability to support more complex groundwater ecosystems) depends on the size and density of openings in the rock, as these, together with the lithology, determine the amount of space and the ambient water chemistry present in the subsurface (Goldscheider et al., 2006). Habitat quality in unconsolidated sediments depends on pore space size, and is generally better in coarse-grained aquifers (Dole-Olivier et al., 2009; Hahn, 2009; Hahn & Fuchs, 2009; Malard et al., 2009). In fractured rocks, habitat quality is highly variable and depends on fracture size, density and connectivity (Hahn & Matzke, 2005; Hahn & Fuchs, 2009; Maurice & Bloomfield, 2012). Karstic rocks generally have high habitat quality, because dissolution has transformed fractures into large voids and cave systems with rapid water flow and surface connectivity (Danielopol et al., 2004; Malard et al., 2009; Robertson et al., 2009).

Grouping of habitats is frequently done for surface ecosystems and plays an essential role in ecology and conservation (Russ & Montgomery, 2002; Canadas et al., 2005; Russo et al., 2005). In groundwater ecosystem studies, geologies have generally been amalgamated into broad habitat categories (e.g. Castellarini et al., 2007; Dole-Olivier et al., 2009; Hahn & Fuchs, 2009; Robertson et al., 2009; Johns et al., 2015). While fractured rocks are generally characterised by communities of low diversity and abundance (Hahn & Fuchs, 2009), karstic and porous rocks have been found to harbour more complex communities with higher diversity and abundance of both invertebrates and microbial biocenoses (Goldscheider et al., 2006; Robertson et al., 2009; Stoch et al., 2009; Gibert et al., 2009). At the continental scale, a groundwater habitat map based on the European hydrogeological map has been developed (Cornu et al., 2013).

The quality of groundwater habitats also depends on water chemistry. Dissolved oxygen (DO), dissolved organic carbon (DOC), calcium (Ca) and nitrate (NO_3) influence groundwater ecosystems, and the distribution of stygobites (Datry et al., 2005; Goldscheider et al., 2006; Hahn, 2006; Dole-Olivier et al., 2009; Hahn & Fuchs, 2009; Griebler et al., 2010). Generally, rocks with higher permeability are thought to provide higher levels of oxygen (due to faster groundwater movement) and organic detritus than less permeable rocks (Hahn, 2006; Bork et al., 2009; Maurice & Bloomfield, 2012).

The need for more detailed typologies of groundwater habitats, incorporating hydrogeological and hydrochemical data, has been highlighted (Castellarini et al., 2007; Tomlinson & Boulton, 2010; Larned, 2012; Stein et al., 2012). Grouping geological strata into only a few units reduces the explanatory power of habitat frameworks, a problem which is further exacerbated by the heterogeneity of rocks (Stoch et al., 2009; Larned, 2012). A more detailed approach is necessary to assess species-habitat associations (Datry et al., 2005; Hancock et al., 2005), providing scientists with an improved tool for management and conservation decisions (Hahn, 2009).

This paper aims to

- use lithological and hydrogeological information to develop a geo-habitat typology for England and Wales.
- establish and compare the abiotic conditions (transmissivity, DO, DOC, NO_3 and Ca) in the geo-habitats, and to develop a habitat quality scoring system.
- assess the distribution and connectivity of geo-habitats in England and Wales to provide a framework for future ecological studies.

2. Methodology

2.1 Assessing geo-habitat distribution

Determining geo-habitat categories

Initially bedrock was separated into karstic, porous and fractured rock as in previous studies (e.g. Galassi et al., 2009; Hahn & Fuchs, 2009; Malard et al., 2009; Martin et al., 2009). Further subdivisions were made (Fig. 1), based on differences in hydrogeological features (e.g. karstification, fractures, and pore space sizes), which affect the available habitat space and water chemistry.

Rocks with a mixture of intergranular and fracture water flow were assigned to a mixed rock geo-habitat (Fig. 1, step a). This comprised Mixed Sandstone (mainly of Permo-Triassic age) which has both cemented and unconsolidated sections, dominated by fracture and intergranular flow respectively (Allen et al., 1997). This geo-habitat is characterised by highly variable fracture sizes, fracture density, cementation and mudstone content (Allen et al., 1997).

Karstic aquifers were grouped into four habitats (Fig. 1, step b). These were based on previous classifications that suggest that karstification increases from the Cretaceous Chalk, through Permian limestone, to the Jurassic limestone and then the Carboniferous limestone (Atkinson & Smart, 1981; Worthington & Ford, 2009). Although caves are rare in the Chalk, solutional fissures and small conduits commonly occur (Maurice et al., 2006, 2012). The Permian limestone is dolomitic and mildly karstic in nature. In the Jurassic limestone caves are slightly more common, although the predominant habitat is solutional fissures and conduits. The Carboniferous limestone has extensive cave systems up to 100 km in length, providing caves and solutional fissures as habitat.

Fractured rocks were separated into four geo-habitats (Fig. 1 step c), based on the size and density of fracturing. Fractured Sandstone has a relatively well developed fracture network, supporting moderate permeability (Jones et al., 2000). Igneous Rock and Metamorphic Rock both have low fracture densities, and therefore low permeability (Jones et al., 2000). However, because the groundwater chemistry (e.g. DO and Ca) in Igneous and Metamorphic Rock in the study area differs considerably (Smedley & Allen, 2004; Shand et al., 2005), they were retained as separate geo-habitats. Mudstones & Siltstones are consolidated fine-grained sedimentary rocks, which have limited fracture networks (Jones et al., 2000).

Unconsolidated sediments were divided into Small-Pore Unconsolidated and Large-Pore Unconsolidated sediments based on differences in grain and pore space size (Fig. 1, step d). Sediments with grain sizes below 2 mm (clay, silt, sand) were classified as Small-Pore Unconsolidated (Wentworth, 1922), while sediments with larger grain sizes were classified as Large-Pore Unconsolidated (e.g. gravel, flints, pebbles, boulders) (Jones et al., 2000). More recent Quaternary superficial deposits also form porous habitats, but were not included in this study because there is insufficient information on their physical and chemical properties.

Assigning geological units to geo-habitats

Geological mapping of the UK is available at the 1:625,000, 1:250,000, 1:50,000 and 1:10,000 scales. A scale of 1:50,000 was used as it provides geological detail and accurate geological boundaries. ArcGIS 10.1 (ESRI, 2011) was used to visualise the 10,000 different geological units in England and Wales.

Units were first sorted by age, as this determines lithological features, such as the extent of karstification in carbonate rocks or consolidation in other sedimentary rocks (Worthington & Ford, 2009). Lithologies in the attribute tables (available from BGS; Smith et al., 2013) are sorted by dominance and a geological unit was assigned to the geo-habitat that corresponded to the dominant lithology.

For some geological units, the categorisation was more complex. To decide whether sandstones were included in 'Mixed Sandstone' or 'Fractured Sandstone' information on age, consolidation and flow type was compiled from the BGS online lexicon (http://www.bgs.ac.uk/lexicon) and the aquifer properties manuals for England and Wales (Allen et al., 1997; Jones et al., 2000). As part of the grouping process geological units with different characteristics sometimes had to be included in the same geo-habitat (Table 1).

2.2 Assessing Geo-Habitat Characteristics

Data Collection

Transmissivity and porosity data were obtained from the UK aquifer properties manuals, including 1724 transmissivity values from pumping tests and 518 porosity values (both summary values) from core samples at different locations (see Table 2) (Allen et al., 1997; Jones et al., 2000). The distribution of sites with transmissivity data was uneven across geo-habitats (Fig. S1), as pumping tests are often only performed on successful boreholes with relatively high yields. Porosity samples had less extensive coverage (Fig. S2). Sampling coverage was evenly distributed for Mixed Sandstone and the Chalk, while for other geo-habitats such as Fractured Sandstone and Igneous Rock no data were available from south-west England and south-west Wales, respectively (Fig. S2). There have been few porosity measurements in Small-Pore and Large-Pore Unconsolidated sediments.

Hydrochemical data, including DO, DOC, NO_3 and Ca, were obtained from the British Geological Survey (BGS) and Environment Agency (EA) Baseline Chemistry Report Series of aquifers in the UK (e.g. Ander et al., 2004; Cobbing et al., 2004; Smedley et al., 2004).

Because specific location data were not available for these samples, published reports were used to identify the aquifers the samples came from (British Geological Survey, 2016). These reports predominantly cover the main aquifers, and particularly for Igneous and Metamorphic rocks do not cover the full range of these rocks present in England and Wales. Hydrochemical data from a faunal distribution study in south-west England were also used (Johns et al., 2015). In total 1363 DO samples, 998 DOC samples, 2342 NO_3 samples and 2898 Ca samples were available (see Table 3). For several geo-habitats (e.g. the southern Chalk, Smedley et al., 2003; Moderately Karstic Limestone, Griffiths et al., 2006) some data came from confined sites (i.e. covered by overlying strata of low permeability), which typically have low oxygen and nutrient concentrations not representative of the rest of the aquifer. However, these could not be identified in the anonymised data set, which was therefore used in its entirety.

Some of the DO concentrations were very high, possibly due to poor calibration. For DO records from Johns et al. (2015), temperature data were used to determine the maximum possible DO (VLMP, 2016). All values above these thresholds were excluded from the analysis. For DO records from the baseline chemistry reports, temperatures were unavailable and the average groundwater temperature of 10.5 °C from a long-term study (Bloomfield et al., 2013) was used to identify the maximum possible DO of 11.5 mg/L, allowing for a small amount of oversaturation.

Comparing Geo-Habitat Characteristics

Summary statistics of hydrogeological and hydrochemical variables were calculated in R (R Development Core Team, 2017). To determine whether data were normally distributed, histograms, q-q plots and Shapiro-Wilk normality tests were conducted.

As all variables were non-normally distributed, non-parametric Kruskal-Wallis tests were used to test for significant differences between geo-habitats. When these were significant ($P < 0.05$) post-hoc multiple pairwise comparisons with Bonferroni corrections were performed in the R 'Psych' package (Revelle, 2016) to determine which geo-habitats differed. To reduce the number of comparisons, the geo-habitat with the lowest mean transmissivity was used as a point of comparison because this was likely to be the least suitable habitat.

Following Gagic et al. (2016), a principal component analysis was conducted in the R package 'missMDA' (Josse & Husson, 2016) to assess abiotic characteristics in broad habitat groups (karstic, porous, fractured). This package deals with missing values in the dataset by using a regularised mean substitute method, which takes the parameter mean and correlations between variables into account (Josse & Husson, 2012). As the PCA was conducted on mixed-type data, categorical variables were transformed into a disjunctive data table, before being scaled to unit variance using MCA scaling (Josse & Husson, 2012).

2.3 Evaluation of Geo-Habitat Quality:

To assess the quality of geo-habitats, 7 parameters known to influence groundwater communities were considered. These were DO (Gibert et al., 1994; Dole-Olivier et al., 2009), DOC (Datry et al., 2005; Hahn, 2006), NO_3 (Stein et al., 2010), Ca (Rukke, 2002), transmissivity (permeability) (Hahn, 2006; Bork et al., 2009), cave development (Culver & Sket, 2000) and physical habitat space (Dole-Olivier et al., 2009). A method was developed to determine overall habitat suitability. Critical parameter thresholds (below which ecosystem health would be likely impaired) were identified using previous studies. These thresholds were used as cut-off points to identify the ratio of good to bad quality patches.

Identification of thresholds and additional parameters

A critical threshold of 1 mg/L was set for DO, as previous studies found this concentration to be the lower critical survival limit of groundwater invertebrates (Malard & Hervant, 1999; Hahn, 2006). For DOC, the main food source in groundwater, a critical threshold of 0.4 mg/L was used, because this was the concentration below which taxa were lost from groundwater communities in a study by Datry et al. (2005). For NO_3, an important additional resource for bacteria (Stein et al., 2010), the threshold was set to 1 mg/L (as NO_3-N) because lower concentrations limit the reproductive capacity of some groundwater bacteria (Rivett et al., 2008). Ca was set at a critical limit of 5 mg/L, because this was the minimum concentration needed for surface freshwater invertebrates to maintain their carapace (Rukke, 2002). For transmissivity, a lower threshold of 52 m^2/d was set, which was the average transmissivity in Mudstones & Siltstones (Jones et al., 2000) that typically support depauperate communities (Hahn & Fuchs, 2009; Johns et al., 2015).

Cave development was considered, because caves provide particularly good groundwater habitats (Culver & Sket, 2000; Robertson et al., 2009). Physical habitat space was incorporated because it is known to affect faunal distributions. For example, pore space size is known to limit groundwater assemblages by excluding larger invertebrates from habitats (Dole-Olivier et al., 2009).

Calculation

(a) The ratio of the number of sites above threshold (*A*) / below threshold (*B*) was calculated for all parameters (*i*) in each geo-habitat. The mean of each parameter was ranked between all geo-habitats from 1 (lowest mean) to 11 (highest mean). The threshold ratio for each parameter was multiplied with the rank of its mean (*Rm*) to give a habitat score for each parameter. Values for all parameters were then summed to give an intermediate habitat score (*IS*, *eqn 1*).

$$IS = \sum_{i=1,2,3,4,5} \left(\frac{A}{B}.Rm \right) \qquad (1)$$

(b) Each geo-habitat received a cave score (*CS*) between 1 (no caves) and 4 (extensive caves). Furthermore, geo-habitats either received a penalty score (*SP*) of 1 (physical space not limiting) or 2 (physical space excluding larger fauna). The *IS* of each geo-habitat was multiplied with the cave score and divided by the space penalty to give the final geo-habitat quality score (*FS, eqn 2*).

$$FS = \frac{IS.CS}{SP} \qquad (2)$$

3. Results

Distribution of geo-habitats

Overall, the total coverage of broad habitat groups varies considerably. Fractured rocks are the most common type of groundwater habitat (62.4 %), whereas karstic (19 %) and porous / mixed habitats (18.6 %) cover much smaller areas.

The distribution of the 11 geo-habitats is uneven across England and Wales (Fig. 2). Three geo-habitats (Mudstones & Siltstones, Fractured Sandstone and the Karstic Chalk) clearly dominate, covering areas of 36.9 %, 20.6 % and 10.7 % respectively. The karstic Chalk forms a continuous band in eastern England, running from north to south (Fig. 2). Conversely, Mudstones & Siltstones, and Fractured Sandstone have a much more dispersed and patchy distribution (Fig. 2).

Other karstic habitats, such as the Mildly and Moderately Karstic Limestone, are also prevalent across extensive areas of central, southern and eastern England. They form continuous belts running on a north-south axis. Such belts are absent from Wales and south-western England, where Highly Karstic Limestone occurs in isolated patches. Porous and mixed geo-habitats, such as Large-Pore Unconsolidated sediments and Mixed Sandstone are almost entirely restricted to England and generally have a patchy distribution. An exception are Small-Pore Unconsolidated sediments in eastern England, which are geographically extensive (Fig. 2). Fractured habitats occur widely in Wales, south-west, central and north-west England (Fig. 2). All fractured habitats are relatively discontinuous, but differ greatly in their distribution. Igneous and Metamorphic Rock are relatively uncommon habitats limited to Wales, south-west and northern England. Fractured Sandstone and Mudstones & Siltstones are widespread.

While some geo-habitats cover extensive areas, others such as Highly Karstic Limestone (2.8 %), Large-Pore Unconsolidated sediments (1 %) and Mildly Karstic Limestone (1 %) cover only small parts of England and Wales. Overall, the geo-habitats therefore range from widespread and well connected to rare and isolated.

Geo-habitat characteristics

The PCA ordination indicated that geo-habitat was strongly associated with transmissivity (T) (Fig. 3a): Fractured geo-habitats were characterised by low T, porous geo-habitats by intermediate T and karstic geo-habitats by high T (Fig. 3b). Geo-habitats were clearly distinguishable by broad habitat type (karstic, porous and fractured) on the PCA biplot, with ellipsoids indicating a marginal difference in abiotic conditions between karstic and porous geo-habitats, while showing significant abiotic differences to fractured geo-habitats (Fig. 3c).

The first principal component axis (15.99 % explained variance) indicated that karstic and porous geo-habitats, grouped on the upper right of the ordination (Fig. 3c), had higher transmissivity, DOC, NO_3 and Ca than fractured geo-habitats (Fig. 3). The exception was Highly Karstic Limestone, which was separated from the other karstic habitats and had lower concentrations of these parameters.

The second principal component axis (13.78 % explained variance) was characterised by a positive loading of DO (Fig. 3a). Karstic and fractured geo-habitats were characterised by higher DO concentrations than porous geo-habitats (Fig. 3). Again, Highly Karstic Limestone differed from other karstic habitats and had a lower DO concentration. Overall, the PCA confirmed that a broad typology produces distinguishable karstic, porous and fractured groups, but that some geo-habitats do not follow the general patterns.

Hydrogeology

The geo-habitats had significantly different transmissivity (Kruskal-Wallis test: H(10) = 799.58, $P < 0.001$, Fig. 4). The highest mean transmissivities occurred in karstic geo-habitats, such as Moderately Karstic Limestone and the Chalk (1504 m^2/d) (Fig. 4, Table 2). Medium transmissivities were found in Mildly Karstic Limestone, Large Pore Unconsolidated and Mixed Sandstone. The lowest transmissivities occurred in two fractured geo-habitats: Igneous Rock (13 m^2/d) and Metamorphic Rock (16 m^2/d). Highly Karstic Limestone had a similar transmissivity to Small-Pore Unconsolidated sediments.

Minimum transmissivities were similar between geo-habitats, ranging between 0.1 and 1.8 m^2/d. Maximum transmissivities varied between 50 and 25,000 m^2/d (Table 2). Overall, the transmissivity maxima were much lower in fractured geo-habitats than in karstic and porous rocks. Transmissivity was highly variable in all geo-habitats (Fig. 4) and varied over several orders of magnitude in the Chalk (Table 2, Fig. 4). The variability was highest in karstic and porous habitats, and much lower in fractured rocks. The transmissivity in fractured geo-habitats was always low, while karstic and porous habitats had many high transmissivity sites.

Porosity was also significantly different between geo-habitats (H(10) = 206.5, $P < 0.001$, Fig. 4). In unconsolidated and mixed habitats, such as Large-Pore, Small-Pore Unconsolidated sediments and Mixed Sandstone the mean porosity was high (> 24 %). In contrast, consolidated geo-habitats (except the Chalk; 33.8 %) had much lower porosity (< 17 %). With a porosity of 1.5 %, Igneous Rock had the lowest recorded value (Fig. 4, Table 2).

Hydrochemistry

DO concentrations differed significantly between geo-habitats (H(10) = 173.43, $P < 0.001$, Fig. 5). The highest mean DO concentrations occurred in Metamorphic Rock, Igneous Rock and the Chalk. The lowest DO concentrations occurred in Mildly Karstic Limestone, Small-Pore Unconsolidated and Large-Pore Unconsolidated sediments. Most porous geo-habitats had lower DO than fractured habitats (Fig. 5, Table 3). Geo-habitats had minimum DO concentrations between 0.02 and 0.5 mg/L, and maximum DO concentrations between 9.3 and 12.6 mg/L.

DOC concentrations also significantly varied between habitats (H(10) = 82.8, $P < 0.001$, Fig. 5). The highest mean DOC was found in the Chalk and Moderately Karstic Limestone, two karstic habitats, and in Mudstones & Siltstones (Fig. 5, Table 3). Porous and mixed habitats, such as Mixed Sandstone, had intermediate DOC concentrations. DOC was lowest in fractured habitats, such as Igneous Rock and Metamorphic Rock (Fig. 5). Minimum DOC concentrations in geo-habitats ranged between 0.1 to 0.8 mg/L, while the maximum DOC of 292 and 207 mg/L occurred in the Chalk and Moderately Karstic Limestone.

NO_3 concentrations were significantly different between geo-habitats (H(10) = 397.38, $P < 0.001$, Fig. 5). The highest mean NO_3 concentrations occurred in the Small-Pore Unconsolidated, Large-Pore Unconsolidated and Moderately Karstic Limestone geo-habitats (Fig. 5, Table 3). The lowest NO_3 concentrations occurred in fractured geo-habitats, such as Mudstones & Siltstones and Fractured Sandstone (Fig. 5). Minimum NO_3 in habitats ranged between 0.002 to 0.1 mg/L, while the maximum NO_3 varied considerably between 12.7 and 72 mg/L.

Ca also varied significantly between habitats (H(10) = 1244.8, $P < 0.001$, Fig. 5). The highest Ca concentrations occurred in the Chalk, Moderately Karstic Limestone and Large-Pore Unconsolidated sediments (Fig. 5, Table 3). The lowest mean Ca concentrations occurred in fractured habitats, such as Igneous Rock and Mudstones & Siltstones (Fig. 5). Minimum Ca was fairly consistent between 0.5 and 14.2 mg/L, while maximum Ca concentrations ranged between 66.2 and 795 mg/L.

Geo-habitat quality

The scores suggest that habitat quality varies considerably among geo-habitats (Fig. 6). The highest quality score was obtained for the Chalk and the lowest for Metamorphic Rock. For discussion purposes, geo-habitats were assigned to three broad groups with high (> 4.5), intermediate (4 – 4.5) and low (< 4) quality. The high quality group includes the Chalk and Highly Karstic Limestone, two karstic geo-habitats (Fig. 6). The intermediate group includes two karstic (Mildly Karstic Limestone, Moderately Karstic Limestone), one mixed (Mixed Sandstone) and one porous (Large-Pore Unconsolidated) geo-habitat (Fig. 6). The low quality group comprises one porous geo-habitat (Small-Pore Unconsolidated) and the fractured geo-habitats (Mudstones & Siltstones, Igneous Rock, Fractured Sandstone, Metamorphic Rock) (Fig. 6).

The distribution map with habitats grouped according to their quality shows that low quality habitats are dominant in Wales, northern and south-west England (Fig. 7). High quality, and some medium quality, habitats provide highly permeable corridors connecting southern to northern England. Medium quality habitats cover small geographical areas and are spatially patchy, particularly in Wales and southern England.

4. Discussion

Assessing the new typology

In this study the classical approach of dividing habitats into karstic, porous and fractured rocks was refined to produce a higher resolution typology of 11 geo-habitats. These geo-habitats differ significantly in their hydrogeological and hydrochemical characteristics, supporting this typology. The differences are likely to influence groundwater communities (Gibert et al., 1994; Datry et al., 2005; Hahn, 2006; Schmidt & Hahn, 2012), illustrating the advantage of this higher resolution. However, all abiotic parameters remain highly variable within geo-habitats, reflecting geological heterogeneity. This transmissivity and resource patchiness are likely to be the cause of the uneven distribution of groundwater fauna observed in many studies (Gibert et al., 1994; Datry et al., 2005). For example, preferential flowpaths at the scale of 10^{-2}- 10^{2} metres may determine the oxygen and food supply for microbes and metazoans in rocks (Stanford et al., 1994; Harvey, 1997; Larned, 2012). Therefore, even more detailed geological data are needed to explain faunal distributions in regional-scale and local-scale studies.

While high geological resolution is important, grouping of similar habitat types is necessary because it is impossible to sample 100's of habitats individually. Any habitat typology needs to balance grouping with capturing habitat differences that are relevant to organisms. For a national scale study, the standard habitat groups (karstic, porous, fractured) may be too coarse to accurately assess habitat suitability. For example, fractured Igneous Rock in south-west England supports complex ecological communities, including frequent occurrences of the endemic *Niphargus glenniei* (Knight, 2009; Johns et al., 2015). In contrast, stygobites are much scarcer in Fractured Sandstone (Weitowitz, 2017).

Combining fractured rocks into a single habitat category (e.g. in Hahn & Fuchs, 2009; Cornu et al., 2013) means that substantial differences in habitat are overlooked. At the national scale, 11 geo-habitats appear to be a good compromise of feasibility and resolution, and a similar typology could be used in other geographical areas.

Geo-habitat characteristics and quality

Although porosity is important in determining space provision and nutrient delivery in unconsolidated habitats (Hahn, 2006; Hahn & Fuchs, 2009), it is a poor proxy of habitat quality. For example, the Chalk has a high mean porosity of 34 % (Allen et al., 1997), but groundwater fauna are too large to live in its small pore spaces (median 0.49 µm; Price et al., 1976). Pore space size is more important in unconsolidated sediments, determining both physical space and permeability. However, even in porous rocks, high porosity does not necessarily reflect high habitat quality. For example, some Small-Pore Unconsolidated sediments (e.g. clays) may have a similar porosity to Large-Pore Unconsolidated sediments (e.g. gravels), yet the effective porosity contributing to fluid flow may be almost zero (Ezekwe, 2010), and the void spaces too small to provide a habitat.

Transmissivity provides a better habitat quality proxy because it integrates habitat information on multiple scales. It influences habitat chemistry (Hahn, 2006; Hahn & Fuchs, 2009; Robertson et al., 2009), and reflects fracture and fissure size, frequency and connectivity. However, transmissivity data are obtained from borehole tests and therefore in karst aquifers where caves are the best habitat, it may be a poor indicator of habitat quality. For example, the Highly Karstic Limestone harbours abundant groundwater assemblages in extensive cave systems in England and Wales (Robertson et al., 2009; Knight, 2011; Johns et al., 2015), but has a relatively low mean borehole transmissivity (317 m^2/d). Furthermore, transmissivity is only measured in successful abstraction boreholes, biasing available data to the more permeable sections of aquifers (Allen et al., 1997). The overall habitat quality depends on how extensive and connected the more transmissive areas are. Future studies could consider the number, yield and distribution of abstraction points in specific geologies, as these may reflect the extent of high quality habitat patches.

Although more permeable rocks generally have higher levels of oxygen and nutrients (Hahn & Fuchs, 2009), this was not always the case in the geo-habitats. While the water chemistry data are probably representative for most geo-habitats, there may be some sampling biases. For example, it is likely that the low mean DOC in Highly Karstic Limestone was due to water chemistry being measured in boreholes rather than caves, with DOC being considerably higher in the latter (e.g. up to 4 mg/L, Simon et al., 2007; Ban et al., 2008). The mean DO in Mildly Karstic Limestone was relatively low, probably due to samples from anoxic boreholes confined by low permeability overlying strata (Allen et al., 1997). The high DO concentrations in Metamorphic and Igneous Rock may reflect a sampling bias towards shallow, unconfined sources, rather than a widespread occurrence of high DO throughout these geo-habitats.

However, the high mean DO in Metamorphic and Igneous Rock, and the high mean DOC in Mudstones & Siltstones suggest that these geo-habitats contain at least some fracture networks with conditions that are likely to be suitable for groundwater fauna, even though these geologies are generally regarded as poor habitats (Cornu et al., 2013) and barriers to dispersal (Johns et al., 2015). An analysis of stygobite distribution data showed that four of the eight stygobite species in England and Wales occur in Mudstones &

Siltstones, although occurrences were extremely low and sometimes limited to a single record (Weitowitz, 2017).

Every geo-habitat in England and Wales should have the potential to support complex groundwater communities in places, as the mean hydrochemical conditions are above currently known thresholds for groundwater ecosystems (see Rukke, 2002; Datry et al., 2005; Hahn, 2006). The differences in habitat quality are most likely determined by the frequency and extent of poor quality habitat patches, also limiting dispersal. Geo-habitat areas with minimum transmissivities below 2 m^2/d, and DO and DOC concentrations below 1 mg/l and 0.4 mg/l respectively, are likely to harbour fewer invertebrates (Malard & Hervant, 1999) and lower biodiversity (Datry et al., 2005). Taking habitat patchiness into account appears to be crucial in developing new habitat typologies, assessing habitat quality and understanding species distributions. However, due to the data bias towards more permeable aquifer sections, and the high degree of aquifer heterogeneity, this remains challenging.

Given the importance of the included abiotic parameters to groundwater ecosystems, the geo-habitat quality scores are expected to relate to resident community complexity. Low quality geo-habitats should harbour lower species diversity and abundance than high quality geo-habitats. Although the proposed typology is yet to be validated with ecological data, the quality scores are mostly in agreement with biological data from similar habitat types. The Chalk and the Highly Karstic Limestone, the best geo-habitats, are known to harbour significant proportions of the UK groundwater biodiversity (Arietti & Edwards, 2006; Johns et al., 2015; Maurice et al., 2015). Fractured geo-habitats were grouped as low quality habitats and are typically characterised by less diverse communities (Hahn &

Matzke, 2005; Hahn & Fuchs, 2009; Johns et al., 2015). However, there are clear quality differences between fractured geo-habitats. Igneous Rock, previously classified as unsuitable (Cornu et al., 2013), scored considerably higher than other fractured geo-habitats (e.g. Metamorphic Rock, Fractured Sandstone), which is supported by the significant faunal assemblages (including the endemic *N. glenniei*) found there (Johns et al., 2015). Small-Pore Unconsolidated sediments were classified as a low quality geo-habitat, although porous aquifers harbour high biodiversity elsewhere (e.g. Eberhard et al., 2005; Castellarini et al., 2007; Griebler et al., 2010). In Small-Pore Unconsolidated sediments, grains only range between 0.06-0.25 mm in fine sands and up to 2 mm in coarse sands (Wentworth, 1922), with pore spaces likely excluding all larger metazoans (e.g. Dole-Olivier et al., 2009).

While the geo-habitat scores account for the relative proportion of good and bad habitat patches, the chemical requirements of many groundwater organisms, particularly critical thresholds, are not well known (Larned, 2012). More research is needed to determine their abiotic requirements and to develop methods of incorporating geological heterogeneity in habitat assessments.

Distribution of geo-habitats

The low connectivity of groundwater habitats is a key control on faunal distributions, causing them to remain static for long periods of time (Culver et al., 2009; Galassi et al., 2009; Robertson et al., 2009; Johns et al., 2015). In England and Wales, most complex groundwater ecosystems are likely to occur in karstic or porous geo-habitats (except for Small-Pore Unconsolidated sediments). Whilst karstic geo-habitats in this region all harbour abundant stygofauna, communities in porous and mixed habitats seem to be more limited

(Robertson et al., 2009; Johns et al., 2015; Weitowitz, 2017). The highly transmissive karstic belts in south-east England should facilitate the north-south dispersal of species. Nevertheless, many species remain absent from northern England, which is thought to be due to the impacts of the Devensian glaciation (Proudlove et al., 2003; Robertson et al., 2009; Maurice et al., 2015), and suggests low dispersal rates even within these connected aquifers.

Fig. 7 shows that over 60 % of England and Wales is covered by low quality fractured geo-habitats, interspersed between the smaller outcrops of karstic rocks. These extensive outcrops of less suitable habitats are likely to have substantial ecological significance. They have been shown to harbour lower species diversity and abundance (Johns et al., 2015; Weitowitz, 2017), and are likely to limit species dispersal, particularly on the east-west axis. For example, the endemic *N. glenniei* may remain limited to Igneous and Metamorphic Rock in south-west England by a barrier of Mudstones & Siltstones, preventing dispersal to central England (Johns et al., 2015).

Hyporheic zones and some of the more permeable superficial deposits (e.g. alluvium and river terrace deposits in south-west England; Smedley & Allen, 2004) are likely to provide important additional habitats for groundwater organisms. For example, they may have facilitated the dispersal of *N. aquilex*, which has a much wider distribution than other UK stygobite species (Ward & Palmer, 1994; Robertson et al., 2009; Johns et al., 2015). These habitats were not considered in the analysis, because little hydrogeological information and no chemistry data are available for them.

5. Conclusion

This paper developed a new national-scale habitat typology for England and Wales, in which 11 geo-habitats were defined. These had significantly different hydrogeological and hydrochemical characteristics, validating the categorisation and suggesting this may be an appropriate number of habitats for national-scale evaluations. The considerable within-habitat variation illustrates the heterogeneity of groundwater habitats, and the need for even higher resolution hydrogeological data in regional and local groundwater ecosystem surveys. The use of thresholds and habitat quality scores may be useful for assessing habitats in other areas, and could be applied at local, regional and national scales.

Substantial parts of England and Wales are covered by low quality, mainly fractured, geo-habitats that provide limited physical space and little connectivity. This may result in reduced biodiversity in comparison to other countries that have more extensive areas of good quality habitats. The more complex ecosystems are likely to occur in the higher quality habitats, which should receive prioritised attention in conservation. However, low quality habitats may be important locally. For example, the Igneous Rock geo-habitat in south-west England harbours the endemic *N. glenniei*.

This habitat typology provides a framework for ecosystem evaluation in England and Wales, which needs to be tested using ecological data. Similar typologies could be used as a framework for evaluating groundwater ecosystems in other geographic regions.

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Tables

Table 1: Summary of the main lithologies and geological formations contained within each geo-habitat and their geological age range. Geological periods from which most units in a geo-habitat are derived from are marked in **bold**.

Geo-Habitat	Some of main lithologies and formations contained	Geological periods
Karstic Chalk	all chalk	**Cretaceous**
Mildly Karstic Limestone	limestone, dolostones	**Permian**
Moderately Karstic Limestone	oolite, Corallian limestones	**Jurassic** - Cretaceous
Highly Karstic Limestone	limestone, calcarenite, dolomitised limestone, dolostones	Neoproterozoic - **Carboniferous**
Small-Pore Unconsolidated	clay, sand, sand + clay, mud, silt	Cretaceous - **Quaternary**
Large-Pore Unconsolidated	gravel, sand + gravel	Cretaceous - **Quaternary**
Mixed Sandstone	Sherwood Sandstone Group, Kinnerton Sandstone Formation, Tunbridge Wells Sand Formation	**Permo-Triassic-Cretaceous**
Fractured Sandstone	Old Red Sandstone, Crackington Formation, Millstone Grit, wacke	Neoproterozoic - Jurassic
Igneous Rock	andesite, basalt, gabbro, granite, lava, tuff	Neoproterozoic - Permian
Metamorphic Rock	gneiss, mylonite, quartzite, schist, slate	**Neoproterozoic** - Triassic
Mudstones & Siltstones	Aylesbeare Mudstone Group, Mercia Mudstone Group	Neoproterozoic - Cretaceous

Table 2: Number of samples, mean values, standard errors, minimum and maximum values of transmissivity and porosity for each of the geo-habitats. Arrows indicate significantly higher ↑ or lower ↓ levels of a parameter than the 'control' geo-habitat Igneous Rock according to multiple pairwise comparisons (Bonferroni corrected).

Geo-Habitat	**Transmissivity (m^2/d)**				**Porosity (%)**			
	Number of Sites	**Mean (se)**	**Min**	**Max**	**Number of Sites**	**Mean (se)**	**Min**	**Max**
Chalk	734	1504.2 (91.1) ↑	0.5	25000	80	33.8 (0.9) ↑	14	47.8
Mildly Karstic Limestone	22	502.7 (160.6) ↑	0.4	2800	5	13.5 (2)	9.5	19.7
Moderately Karstic Limestone	82	1628.8(317.6) ↑	0.5	14000	25	17.1 (0.7)	8.1	25.8
Highly Karstic Limestone	33	317.4 (178.7) ↑	0.1	5900	15	4.9 (1.6)	0.3	19.5
Small-Pore Unconsolidated	40	252.1 (85.4) ↑	1.1	2300	4	27.2 (3.7) ↑	17.1	32.8
Large-Pore Unconsolidated	86	581.5 (53) ↑	1.8	2500	1	53.7 (NA) ↑	53.7	53.7
Mixed Sandstone	320	505.6 (41.7) ↑	1.7	6200	328	24.5 (0.4) ↑	4.3	52.9
Fractured Sandstone	147	111.9 (21) ↑	0.1	1800	21	13.2 (1.1)	5.3	21.4
Igneous Rock	13	13.4 (4.7)	0.1	50	4	1.5 (0.9)	0.4	4.1
Metamorphic Rock	71	16.1 (3.9)	0.1	180	0	NA	NA	NA
Mudstones & Siltstones	176	51.7 (9.2)	0.2	1300	35	16.1 (1.4)	2.3	32.8

Table 3: Number of samples, the mean concentration and standard error of DO, DOC, NO_3 and for each of the geo-habitats. Arrows indicate significantly higher $\uparrow$ or lower $\downarrow$ levels of a parameter than the ‘control’ geo-habitat Igneous Rock according to multiple pairwise comparisons (Bonferroni corrected).

Geo-Habitat	**Number of Samples**	**DO (mg/L) (se)**	**Number of Samples**	**DOC (mg/L) (se)**	**Number of Samples**	**NO_3-N (mg/L) (se)**	**Number of Samples**	**Ca (mg/L) (se)**
Mildly Karstic Chalk	294	6.8 (0.2)	247	6.3 (1.7) $\uparrow$	623	7.7 (0.2)	680	110.5 (1.4) $\uparrow$
Mildly Karstic Limestone	36	3.2 (0.5) $\downarrow$	36	2.1 (0.3)	105	3.6 (0.4) $\downarrow$	112	107.7(7.1) $\uparrow$
Moderately Karstic Limestone	107	5.1 (0.3) $\downarrow$	89	6.3 (2.4) $\uparrow$	104	8.6 (0.6)	171	107.7 (3.9) $\uparrow$
Highly Karstic Limestone	100	6.3 (0.3)	98	1.7 (0.2)	181	3 (0.3) $\downarrow$	229	80.4 (2.9) $\uparrow$
Small-Pore Unconsolidated	57	3.2 (0.4) $\downarrow$	60	5.1 (2.3)	31	10.6 (2.7)	73	69 (3.9) $\uparrow$
Large-Pore Unconsolidated	13	4.3 (0.8) $\downarrow$	21	2.1 (0.3)	67	11.6 (1.3)	85	120.1 (7.3) $\uparrow$
Mixed Sandstone	420	4.8 (0.1) $\downarrow$	310	4.1 (0.4) $\uparrow$	682	6 (0.3)	844	97.2 (3.3) $\uparrow$
Fractured Sandstone	115	5.7 (0.3) $\downarrow$	79	1.5 (0.1)	204	2.6 (0.2) $\downarrow$	282	44.6 2.2) $\uparrow$
Igneous Rock	79	7.5 (0.3)	39	1.4 (0.2)	209	6.3 (0.3)	213	14.9 (0.7)
Metamorphic Rock	3	8.1 (1.6)	5	1.8 (0.6)	7	8.5 (3.8)	7	35.4 (6)
Mudstones & Siltstones	139	4.9 (0.3) $\downarrow$	14	5.8 (3.1)	129	2.5 (0.3) $\downarrow$	202	32.2 (2.2) $\uparrow$

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Figures

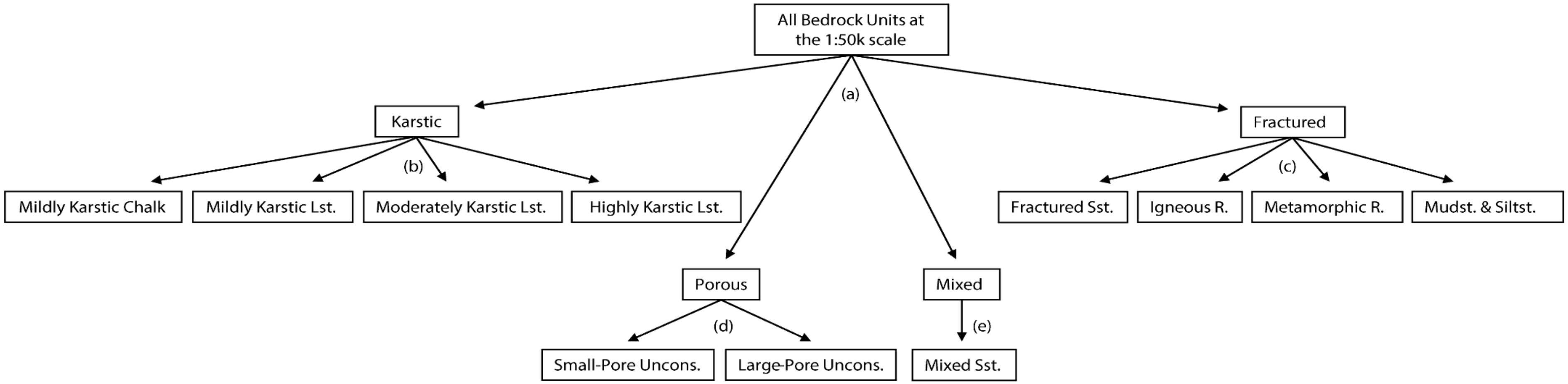
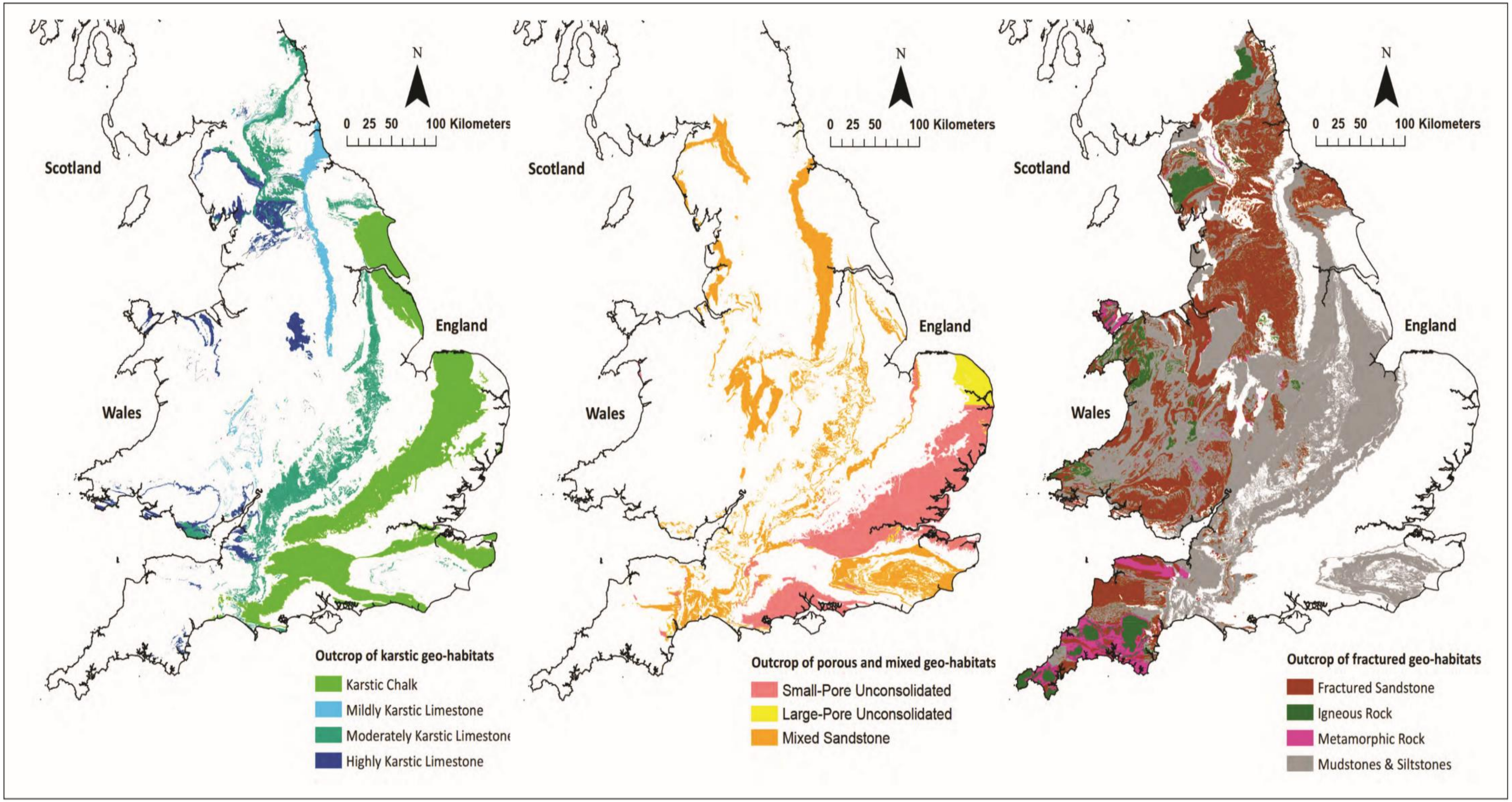


Fig. 1: The geo-habitat categorisation process. Lst. = Limestone, Sst. = Sandstone, R. = Rock, Mudst. & Siltst. = Mudstones & Siltstones, Uncons. = Unconsolidated

787



788 Fig. 2: Distribution maps of the outcrop of groundwater geo-habitats in England and Wales.

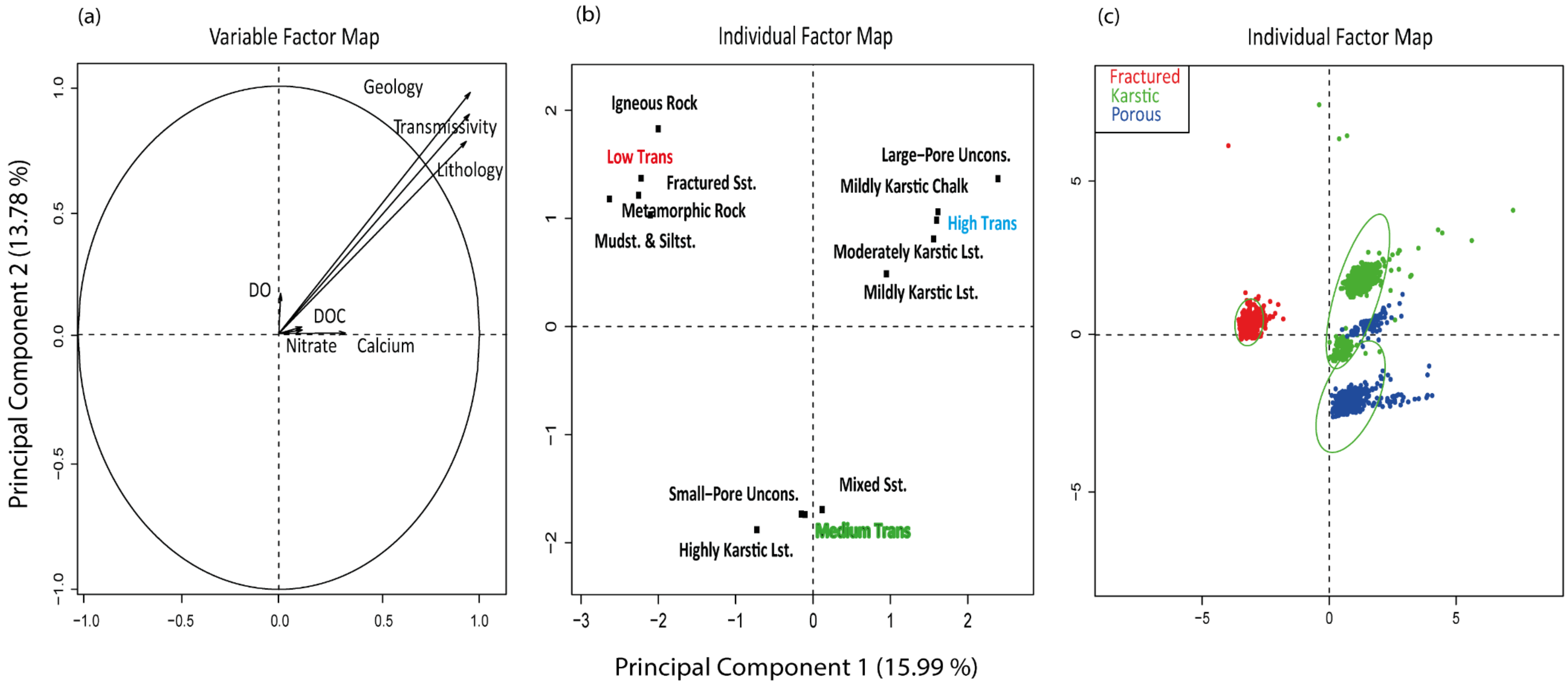


Fig. 3: (a) Ordination of environmental variables in a Principal Component Analysis (PCA), explaining a total of 29.77 % of data variance. (b) Ordination of geo-habitats grouped by different colour-coded transmissivities (low, medium, high). (c) Ordination of broad lithologies (fractured, karstic, porous habitats) with individual colour-coding. Confidence ellipsoids around different groups indicate differences between broad lithologies.

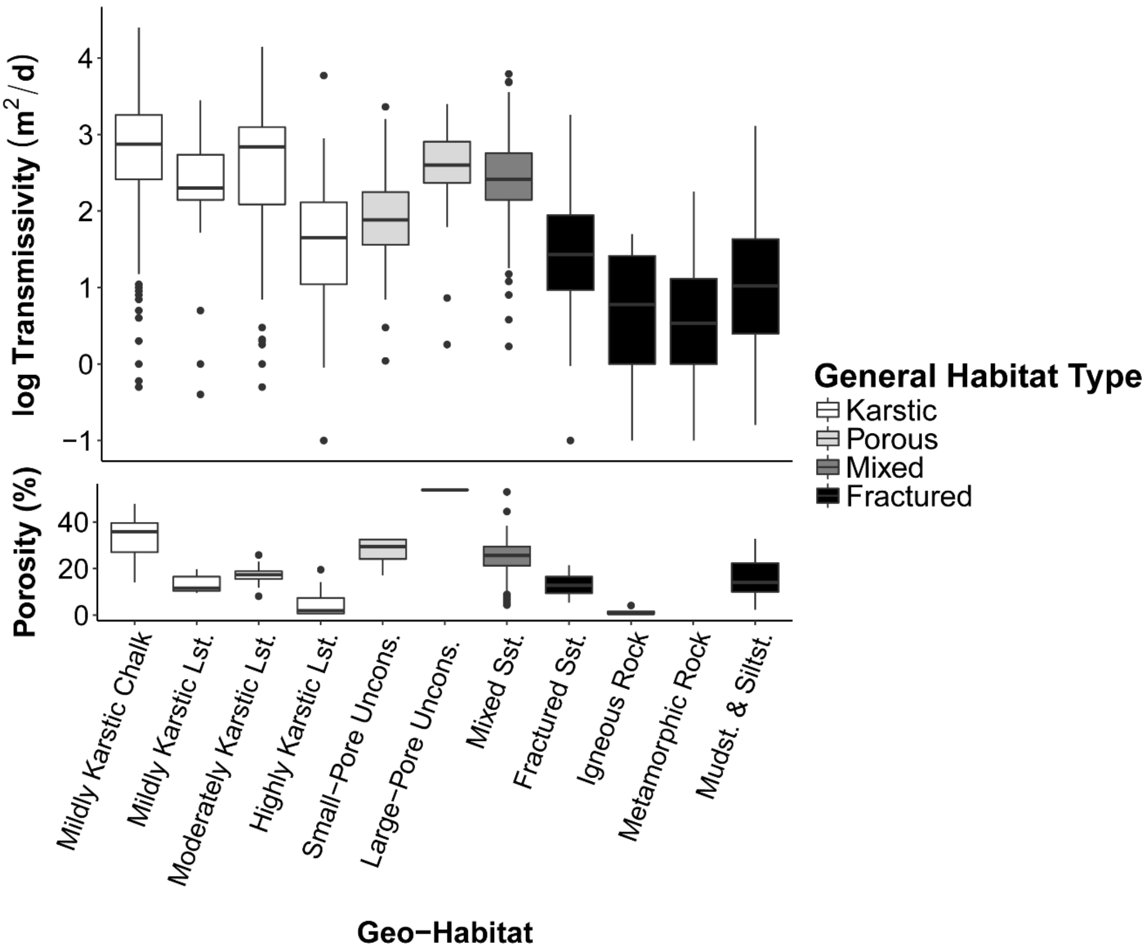


Fig. 4: Hydrogeological variables for the 11 geo-habitats showing (a) log Transmissivity (m^2/d) and (b) Porosity (%), with the horizontal band representing the medium, the bottom and top of the box representing the first and third quartiles, and the whiskers representing one standard deviation above and below the mean. No porosity data was available for Metamorphic Rock. Lst. = Limestone, Sst. = Sandstone, Mudst. & Siltst. = Mudstones & Siltstones

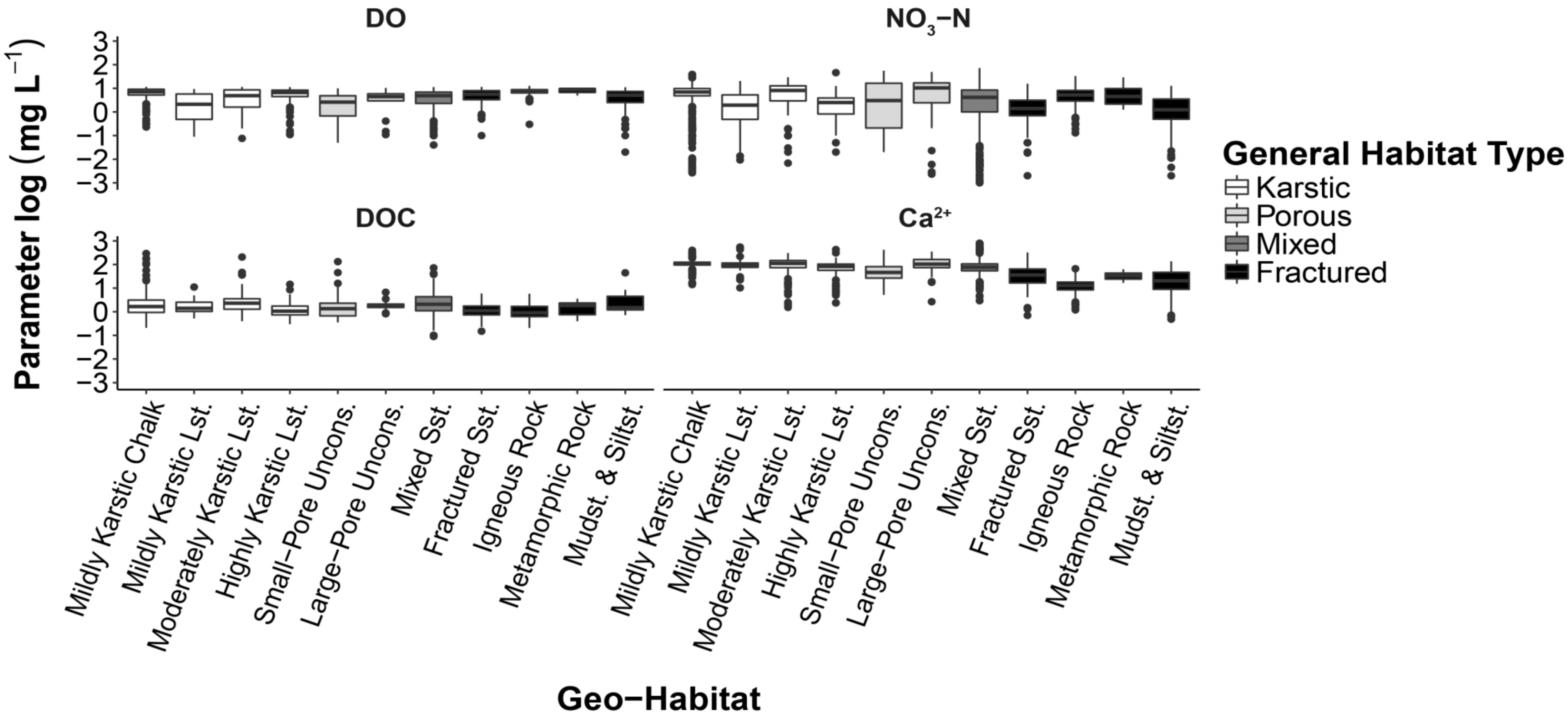


Fig. 5: Hydrochemical variables for the 11 geo-habitats showing logs of DO, DOC, Ca and NO_3 (all in mg/L), with the horizontal band representing the medium, the bottom and top of the box representing the first and third quartiles, and the whiskers representing one standard deviation above and below the mean. Lst. = Limestone, Uncons. = Unconsolidated, Sst. = Sandstone, Mudst. & Siltst. = Mudstone & Siltstone

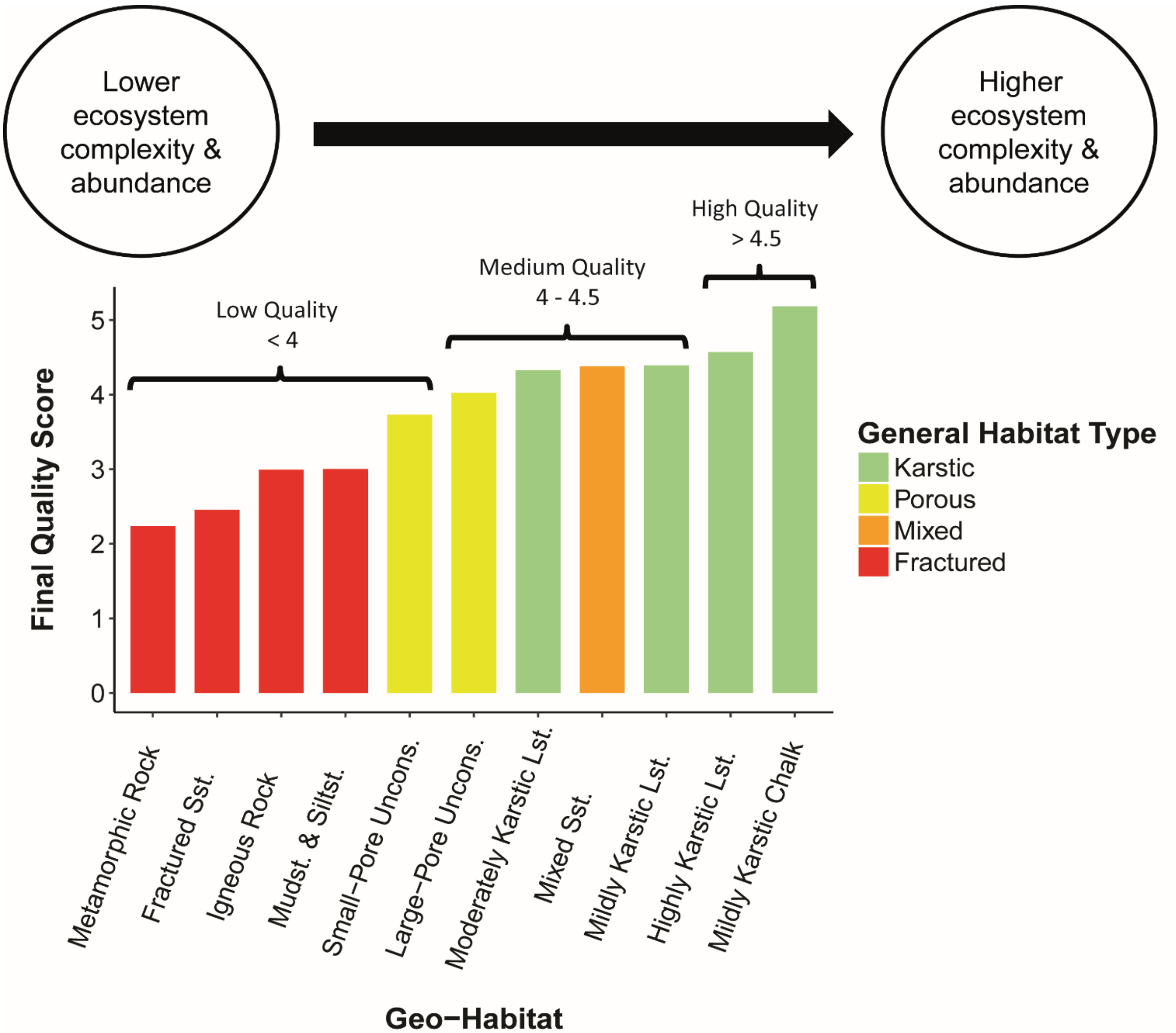


Fig. 6: Log geo-habitat quality scores sorted from lowest to highest.

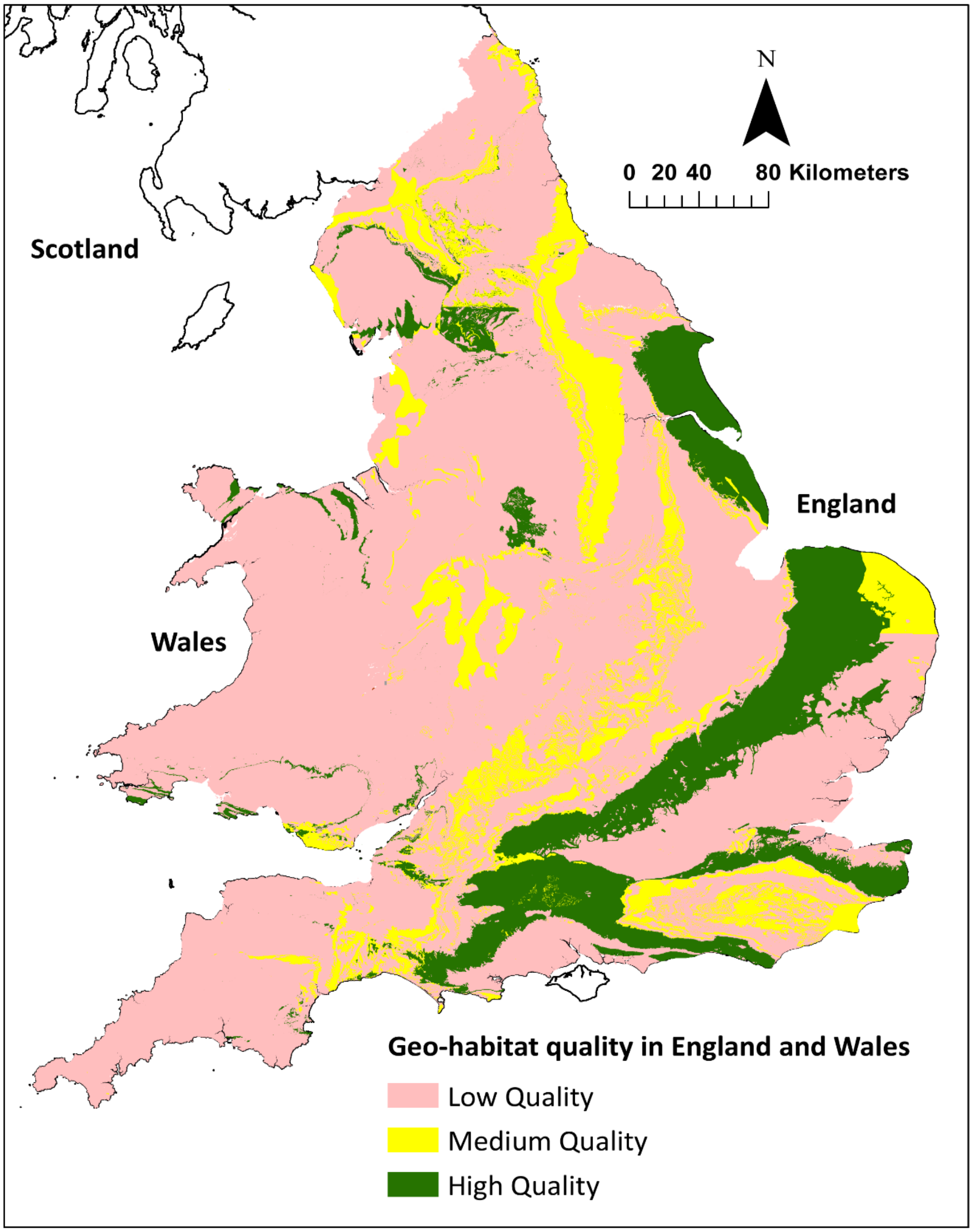


Fig. 7: Distribution map of groundwater habitats in England and Wales grouped by their habitat quality scores calculated from abiotic parameters important to groundwater ecosystems.